Ecological Applications, 23(8), 2013, pp. 1893–1905

A seasonal, density-dependent model for the management of an invasive weed

Esther Shyu,[1,3] Eleanor A. Pardini,[2] Tiffany M. Knight,[2] and Hal Caswell[1]

[1]*Biology Department MS-34, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 USA*
[2]*Department of Biology, Washington University in St. Louis, St. Louis, Missouri 63130 USA*

Abstract. The population effects of harvest depend on complex interactions between density dependence, seasonality, stage structure, and management timing. Here we present a periodic nonlinear matrix population model that incorporates seasonal density dependence with stage-selective and seasonally selective harvest. To this model, we apply newly developed perturbation analyses to determine how population densities respond to changes in harvest and demographic parameters. We use the model to examine the effects of popular control strategies and demographic perturbations on the invasive weed garlic mustard (*Alliaria petiolata*). We find that seasonality is a major factor in harvest outcomes, because population dynamics may depend significantly on both the season of management and the season of observation. Strategies that reduce densities in one season can drive increases in another, with strategies giving positive sensitivities of density in the target seasons leading to compensatory effects that invasive species managers should avoid. Conversely, demographic parameters to which density is very elastic (e.g., seeding survival, second-year rosette spring survival, and the flowering to fruiting adult transition for maximum summer densities) may indicate promising management targets.

Key words: Alliaria petiolata; Ceutorhynchus scrobicollis; *compensatory mortality; density dependence; garlic mustard; harvest; invasive species; periodic matrix models; perturbation analysis; seasonality*.

Introduction

Harvest, the often-selective removal of individuals from a population, appears in many ecological contexts, including maintaining resource species, controlling invasive pests, and anticipating the conservation effects of inadvertent casualties (e.g., bycatch, ship strikes). In each case, modeling the population effects of harvest is crucial for management. These effects are determined by interactions with density dependence, seasonality, stage structure, and management timing.

Density dependence plays a sometimes counterintuitive role in population dynamics. If harvest increases resource availability, mortality due to that harvest may be counterbalanced by density-dependent increases in survival and fertility (compensatory mortality and natality). Harvest may even increase overall density (overcompensation; e.g., Jonzén and Lundberg 1999, Zipkin et al. 2009). Compensation and overcompensation have been observed in many pest species (e.g., Buckley et al. 2001, Jonzén et al. 2002, Zipkin et al. 2008, Pardini et al. 2009) and may underlie the persistence of invasive populations under management.

Seasonality produces dramatic environmental changes that drive the life cycles of many species. Populations thus vary on two time scales: a seasonal time scale that depends on changes within the year, and an interannual time scale that depends on changes between years. The interaction of these two time scales generates rich dynamics that are obscured in strictly interannual models (e.g., Kot and Schaeffer 1984, Åström et al. 1996). The relative timing of seasonal mortality and density-dependent processes can, for instance, produce compensation and overcompensation (Boyce et al. 1999, Jonzén and Lundberg 1999, Ratikainen et al. 2008). Harvest models that neglect seasonality, forcing mortality and density dependence to operate simultaneously (e.g., Sinclair and Pech 1996), often cannot account for compensatory effects.

Stage structure may change significantly depending on both season and harvest. Stage-specific harvest may also interact with density dependence to increase the densities of nontargeted stages and overall population abundances, as shown in both experimental cultures (Nicholson 1957, Cameron and Benton 2004) and field studies (Pardini et al. 2008, Zipkin et al. 2008).

Timing of harvest affects yield, density (Kokko and Lindström 1998, Boyce et al. 1999), and population persistence (Tang and Chen 2004). Timing also influences compensatory effects, in that harvest prior to reproduction often leads to compensation, whereas later harvests are more effective in reducing populations (Buckley et al. 2001, Ratikainen et al. 2008).

Manuscript received 3 October 2012; revised 27 March 2013; accepted 14 May 2013. Corresponding Editor: E. A. Newell.
[3] E-mail: eshyu@whoi.edu

In this paper, we present a harvest model framework that uses periodic nonlinear matrix population models. The model is seasonally explicit and incorporates harvest selectivity with respect to both stage and timing. We use newly developed perturbation analyses for nonlinear matrix models (Caswell 2008, Caswell and Shyu 2012) to obtain the sensitivity and elasticity of population densities (equilibria or cycles, on both seasonal and interannual time scales) to changes in demographic or management parameters.

We apply this modeling framework to garlic mustard (*Alliaria petiolata*), an invasive European weed that is aggressively displacing North American woodland flora. We develop a harvest model to simulate garlic mustard's seasonal dynamics and evaluate the long-term population density effects of various management approaches and demographic perturbations (see Supplement).

Study Species

Garlic mustard (*Alliaria petiolata*; Brassicaceae) is a Eurasian herb that invades North American forests and edge habitats, forming dense monotypic stands and producing allelopathic toxins that displace native flora (Cavers et al. 1979, Nuzzo 1991, Anderson et al. 1996). Because of its tolerance to many growth conditions, extensive seed dispersal, and ability to self-fertilize, this species has become a pervasive weed in the midwestern and northeastern United States and some parts of Canada (Nuzzo 2000). Although vulnerable to at least 69 insect species and seven fungi in its native range (Hinz and Gerber 1998), garlic mustard experiences minimal pressure from North American herbivores and pathogens (Blossey et al. 2001). Its density-dependent survival and fecundity (Pardini et al. 2008) produce compensatory responses that complicate management efforts.

Garlic mustard is an obligate biennial with a life cycle strongly coupled to the seasons (e.g., Cavers et al. 1979, Roberts and Boddrell 1983, Anderson et al. 1996, Nuzzo 2000, Pardini et al. 2008). As shown in Fig. 1, seeds germinate into seedlings from March to May and mature into vegetative rosettes by June. Rosettes overwinter and develop into flowering adults the following March. Mature fruits (seed-containing siliques) develop by June. If plants are clipped in early summer before fruit formation completes, they may resprout with reduced fecundity. Adults die after setting seed. New seeds disperse in the fall and require cold stratification to sprout. Some germinate in the spring, while others remain in a seed bank for up to 10 years (V. Nuzzo and B. Blossey, *personal communication*).

Demographic parameters in our garlic mustard model (Table 1) are based on data from the Tyson Research Center (Eureka, Missouri, USA), a deciduous forest first invaded by garlic mustard in 2000, with supplemental values from other North American studies (Pardini et al. 2008, 2009).

Modeling Seasonality and Density Dependence

Model structure

The model includes seven stages and four seasons, as shown in Fig. 1. As always, these choices are based on major life cycle transitions (e.g., the difference between vegetative and reproductive stages), management targets (e.g., the difference between clipping plants early or late in the growing season), and available data. Note that, as in this example, seasons need not be the same length, and the same stages need not be present in every season.

We write the population vector in season i of year t as $\mathbf{n}_i(t)$, with the structure:

$$\mathbf{n}_i(t) = \begin{pmatrix} \text{new seeds} \\ \text{bank seeds} \\ \text{seedlings} \\ \text{rosettes} \\ \text{flowering adults} \\ \text{fruiting adults} \\ \text{resprouting adults} \end{pmatrix} \tag{1}$$

and collect the demographic parameters from all seasons (summarized in Table 1) in a parameter vector $\boldsymbol{\theta}$. We write the parameter vector in season i as $\boldsymbol{\theta}_i$. If, as in our case, some parameters in $\boldsymbol{\theta}$ have no effect on the dynamics in season i, their value in $\boldsymbol{\theta}_i$ is irrelevant and can be set to 0, e.g., for

$$\boldsymbol{\theta} = (s_1 \;\; s_5 \;\; b_1 \;\; s_2 \;\; a \;\; r \;\; b_2 \;\; s_3 \;\; f \;\; f_r \;\; b_3 \;\; s_4 \;\; v \;\; g_1 \;\; g_2 \;\; b_4)^\top. \tag{2}$$

Here, $\boldsymbol{\theta}_1$ depends only on parameters for the transition from season 1 to 2:

$$\boldsymbol{\theta}_1 = (s_1 \quad s_5 \quad b_1 \quad 0 \quad \ldots \quad 0)^\top. \tag{3}$$

We write the matrix projecting the population from season i to season $i + 1$ as $\mathbf{B}_i[\boldsymbol{\theta}_i, \mathbf{n}_i]$, which allows demography to depend on both the parameters and densities in season i. Because the model is periodic, the matrix $\mathbf{B}_4$ projects from season 4 to 1.

The annual matrix $\mathbf{A}$, which projects the population from one year to the next, is the product of the seasonal projection matrices. For a projection starting in season 1,

$$\begin{aligned} \mathbf{n}_1(t+1) &= \mathbf{B}_4[\boldsymbol{\theta}_4, \mathbf{n}_4(t)]\mathbf{B}_3[\boldsymbol{\theta}_3, \mathbf{n}_3(t)] \\ &\quad \times \mathbf{B}_2[\boldsymbol{\theta}_2, \mathbf{n}_2(t)]\mathbf{B}_1[\boldsymbol{\theta}_1, \mathbf{n}_1(t)]\mathbf{n}_1(t) \qquad (4) \\ &= \mathbf{A}_1\mathbf{n}_1(t) \qquad (5) \end{aligned}$$

where the subscript on $\mathbf{A}_1$ indicates an interannual projection starting in season 1. Similar expressions can be obtained for projections starting in other seasons via cyclic permutation of the matrices (e.g., Caswell 2001:346–376, Smith et al. 2005).

In this formulation, dynamics on the seasonal time scale are given by the sequence of population vectors $\mathbf{n}_1(t)$, $\mathbf{n}_2(t)$, $\mathbf{n}_3(t)$, $\mathbf{n}_4(t)$, $\mathbf{n}_1(t+1)$, and so forth. Dynamics on the interannual time scale are given by the sequence of vectors for a specific season in successive years, e.g., $\mathbf{n}_1(t)$, $\mathbf{n}_1(t+1)$, $\mathbf{n}_1(t+2)$, and so forth. For the garlic

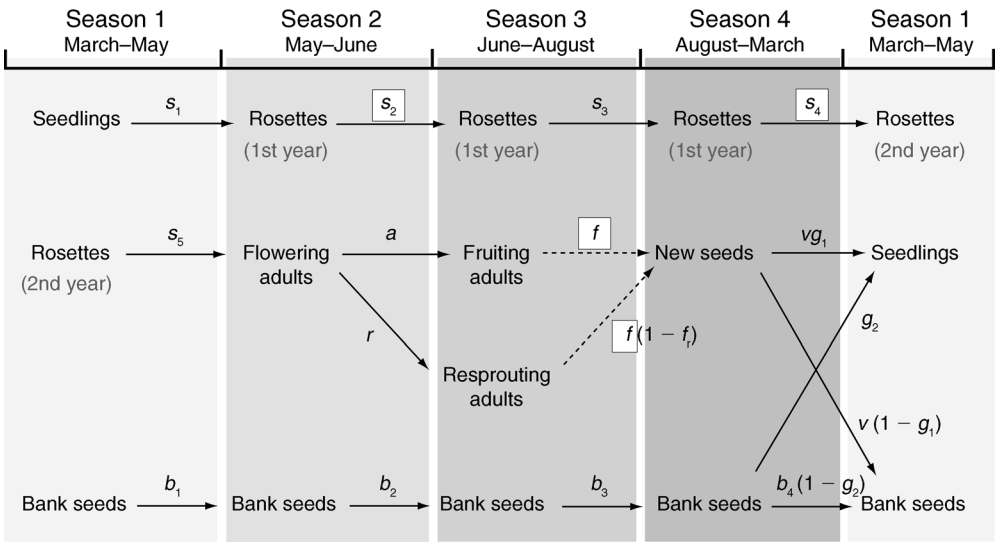

FIG. 1. Life cycle diagram for garlic mustard (*Alliaria petiolata*). Parameters are as shown in Table 1; density-dependent parameters are boxed. Due to garlic mustard's biennial life cycle, two separate cohorts (top and middle) and a seed bank (bottom) are present in each season.

mustard model, which has four seasons, a fixed point on the interannual time scale is a four-cycle on the seasonal time scale with points $\hat{\mathbf{n}}_1$, $\hat{\mathbf{n}}_2$, $\hat{\mathbf{n}}_3$, and $\hat{\mathbf{n}}_4$. A two-cycle on the interannual time scale is an eight-cycle on the seasonal time scale with points

$$\begin{aligned} \hat{\mathbf{n}}_1 &= \mathbf{n}_1(t) & \hat{\mathbf{n}}_5 &= \mathbf{n}_1(t+1) \\ \hat{\mathbf{n}}_2 &= \mathbf{n}_2(t) & \hat{\mathbf{n}}_6 &= \mathbf{n}_2(t+1) \\ \hat{\mathbf{n}}_3 &= \mathbf{n}_3(t) & \hat{\mathbf{n}}_7 &= \mathbf{n}_3(t+1) \\ \hat{\mathbf{n}}_4 &= \mathbf{n}_4(t) & \hat{\mathbf{n}}_8 &= \mathbf{n}_4(t+1). \end{aligned}$$

Although we previously assumed, in Eq. 4, that $\mathbf{B}_i$ is only a function of $\mathbf{n}_i$ (i.e., seasonal projections depend only on density in the current season), density dependence may be delayed if factors in one season affect an individual's status in later seasons (Ratikainen et al. 2008). The $\mathbf{B}_i$ could thus be functions of any seasonal densities over the previous year, for example:

$$\mathbf{B}_1 = \mathbf{B}_1[\boldsymbol{\theta}_1, \mathbf{n}_1(t), \mathbf{n}_4(t-1), \mathbf{n}_3(t-1), \mathbf{n}_2(t-1)]. \quad (6)$$

TABLE 1. Seasonal demographic parameters (Pardini et al. 2008, 2009) and density-dependent functions (Evans and Davis 2011, Pardini et al. 2011) for garlic mustard (*Alliaria petiolata*).

Parameter	Description	Matrix	Value/function
a) Constant parameters			
v	new seed survival	$\mathbf{B}_4$	0.8228
g_1	new seed germination	$\mathbf{B}_4$	0.55034
g_2	bank seed germination	$\mathbf{B}_4$	0.31705
s_1	seedling to 1st-year rosette transition	$\mathbf{B}_1$	0.131
s_3	1st-year rosette survival	$\mathbf{B}_3$	1
s_5	2nd-year rosette to flowering adult transition	$\mathbf{B}_1$	1
a	flowering to fruiting adult transition	$\mathbf{B}_2$	1
r	resprout probability	$\mathbf{B}_2$	0.54
f_r	resprout fertility reduction	$\mathbf{B}_3$	0.95
b_1	bank seed survival	$\mathbf{B}_1$	0.9833
b_2	bank seed survival	$\mathbf{B}_2$	0.9917
b_3	bank seed survival	$\mathbf{B}_3$	0.9917
b_4	bank seed survival	$\mathbf{B}_4$	0.9333
b) Density-dependent parameters			
s_2	1st-year rosette survival	$\mathbf{B}_2$	$1/(1 + \exp - (0.11635 - 0.01612A_2 - 0.00144R_2 - 0.00092A_2R_2))$
s_4	1st-year to 2nd-year rosette transition	$\mathbf{B}_4$	$1/(1 + \exp - (1.32702 - 0.50269\ln(R_4 + 1)))$
f	fertility (seeds/fruiting adult)	$\mathbf{B}_3$	$\exp(7.48933 - 0.03893R_1)$

Notes: Here, A_i and R_i denote the densities of adults and rosettes, respectively, in season i. Functions for s_2 (first-year rosette May–June survival) and s_4 (second-year rosette August–March survival) are based on measurements made in May and August. Due to lack of intermediary data, we have set s_3 (first-year rosette June–August survival), s_5 (second-year rosette March–May survival), and a to 1. Seed bank parameters b_1, b_2, b_3, b_4 were determined assuming temporally uniform decay with complete degradation after 10 years (V. Nuzzo and B. Blossey, *personal communication*).

In practice, it is unlikely that each $\mathbf{B}_i$ will depend on all previous seasonal densities. In the case of garlic mustard, Table 1 shows that $\mathbf{B}_1$ does not depend on density, whereas $\mathbf{B}_2$ and $\mathbf{B}_4$ depend only on densities in the current season. Only $\mathbf{B}_3$ exhibits delayed density dependence, as it contains a fecundity parameter f that depends on season 1 (spring) densities (rosettes that are overcrowded in season 1 become stunted, less fertile adults; e.g., Pardini et al. 2009).

Taking all density effects into account, Eq. 4 can be rewritten for garlic mustard as

$$\mathbf{n}_1(t+1) = \mathbf{B}_4[\boldsymbol{\theta}_4, \mathbf{n}_4(t)]\mathbf{B}_3[\boldsymbol{\theta}_3, \mathbf{n}_1(t)] \times \mathbf{B}_2[\boldsymbol{\theta}_2, \mathbf{n}_2(t)]\mathbf{B}_1[\boldsymbol{\theta}_1]\mathbf{n}_1(t). \quad (7)$$

The four seasonal projection matrices are

$$\mathbf{B}_1[\boldsymbol{\theta}_1] = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & b_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (8)$$

$$\mathbf{B}_2[\boldsymbol{\theta}_2, \mathbf{n}_2(t)] = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & b_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_2[\mathbf{n}_2(t)] & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & a & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (9)$$

$$\mathbf{B}_3[\boldsymbol{\theta}_3, \mathbf{n}_1(t)] = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & f[\mathbf{n}_1(t)] & f[\mathbf{n}_1(t)](1-f_r) \\ 0 & b_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (10)$$

$$\mathbf{B}_4[\boldsymbol{\theta}_4, \mathbf{n}_4(t)] = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ v(1-g_1) & b_4(1-g_2) & 0 & 0 & 0 & 0 & 0 \\ vg_1 & g_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4[\mathbf{n}_4(t)] & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}. \quad (11)$$

Results: seasonal dynamics of unmanaged populations

When parameterized with the values in Table 1, the model produces a stable two-cycle on the interannual time scale, resulting in a biennial eight-cycle on the seasonal time scale (Figs. 2 and 4a). Such interannual two-cycles, i.e., alternating years of high-density vegetative (rosettes, seedlings, bank seeds) and reproductive stages (adults, new seeds), have been observed in both field and experimental studies (Nuzzo 1991, Winterer et al. 2005, Pardini et al. 2009).

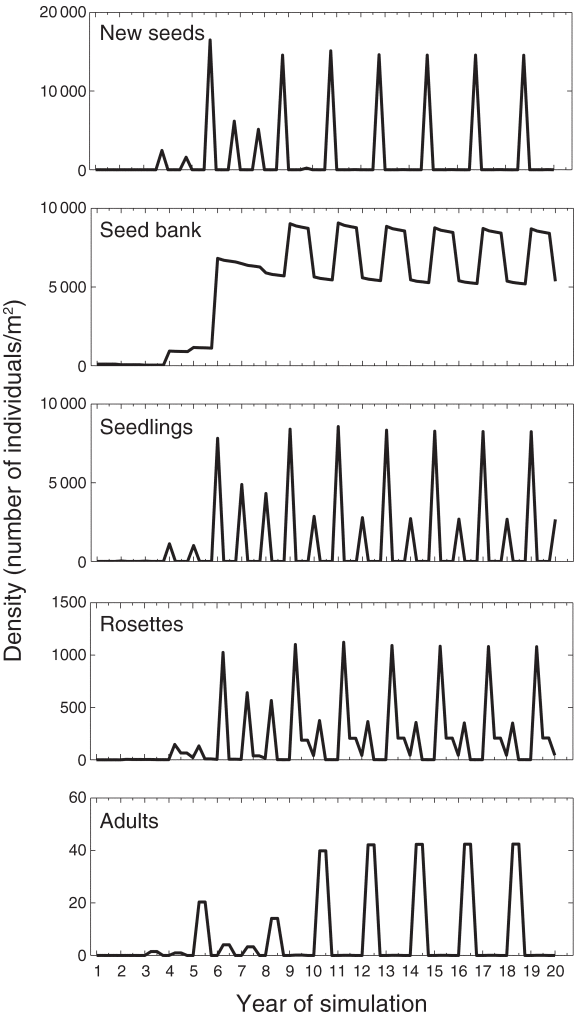

FIG. 2. Simulated dynamics for each stage (individuals per square meter) in an unmanaged garlic mustard population, demonstrating convergence to a seasonal eight-cycle, interannual two-cycle ("adults" refers to the sum of fruiting, flowering, and resprouting stages). Simulations were initialized with 10 bank seeds; reasonable initial distributions (i.e., not consisting only of stages present in other seasons) did not change asymptotic dynamics.

MODELING MANAGEMENT

Management matrices

We describe each management strategy by a matrix $\mathbf{M}$. In most cases, $\mathbf{M}$ only describes survival and is a diagonal matrix with main diagonal diag($\mathbf{M}$) = $\mathbf{m}$. The entries m_i of vector $\mathbf{m}$ give the proportion of stage i

surviving management. However, **M** may also include other transitions induced by management actions. Assuming management is repeated annually, prior to any censuses or density-dependent processes in the managed season, **M** is inserted into the periodic matrix product (7) after the matrix projecting to the managed season. For example, if management occurs every season 1, the post-management season 1 population is given by

$$\mathbf{n}_1(t+1) = \mathbf{M}\mathbf{B}_4\mathbf{B}_3\mathbf{B}_2\mathbf{B}_1\mathbf{n}_1(t) \tag{12}$$

$$= \mathbf{A}_1\mathbf{n}_1(t). \tag{13}$$

We focus on four control strategies, as represented by the following management matrices.

Pulling at ground level can achieve up to 99% mortality of summer flowering plants (Nuzzo 1991). However, this strategy requires intensive hand labor and stem bagging to prevent seed release (Solis 1998, Pardini et al. 2008). We model pulling as a harvest of season 2 flowering adults (reduction by a proportion p_2) using the management matrix $\mathbf{M}_{p_2}$:

$$\text{diag}(\mathbf{M}_{p_2}) = [1, 1, 1, 1, (1-p_2), 1, 1] \tag{14}$$

$$\mathbf{A}_1 = \mathbf{B}_4\mathbf{B}_3\mathbf{B}_2\mathbf{M}_{p_2}\mathbf{B}_1. \tag{15}$$

Clipping at midheight (15 cm above ground) can be done by a single person using a string trimmer, but may also harm native flora. Plants clipped early in the growing season resprout, with reduced fertility, with a probability r (Pardini et al. 2008). Plants clipped later in the season usually cannot resprout, although their stems must be carefully removed to prevent seed dispersal. Management matrices for early clipping (reducing season 2 flowering adults by a proportion c_2) and late clipping (reducing season 3 fruiting adults by a proportion c_3) are

$$\text{diag}(\mathbf{M}_{c_2}) = [1, 1, 1, 1, (1-c_2), 1, 1] \tag{16}$$

$$\mathbf{M}_{c_2}(7,5) = c_2 r \tag{17}$$

$$\mathbf{A}_1 = \mathbf{B}_4\mathbf{B}_3\mathbf{B}_2\mathbf{M}_{c_2}\mathbf{B}_1 \tag{18}$$

$$\text{diag}(\mathbf{M}_{c_3}) = [1, 1, 1, 1, 1, (1-c_3), 1] \tag{19}$$

$$\mathbf{A}_1 = \mathbf{B}_4\mathbf{B}_3\mathbf{M}_{c_3}\mathbf{B}_2\mathbf{B}_1. \tag{20}$$

Herbicides such as glyphosate (Roundup) can be cheaply applied to large areas, but may also kill native species. They are usually used in the early spring, before other species have germinated, or in late fall, when other species are dormant (Nuzzo 1991, 2000, Slaughter et al. 2007). We model spring herbicide as a reduction in season 1 seedlings and rosettes (by a proportion h_1), and fall herbicide as a reduction in season 4 rosettes (by a proportion h_4):

$$\text{diag}(\mathbf{M}_{h_1}) = [1, 1, (1-h_1), (1-h_1), 1, 1, 1] \tag{21}$$

$$\mathbf{A}_1 = \mathbf{M}_{h_1}\mathbf{B}_4\mathbf{B}_3\mathbf{B}_2\mathbf{B}_1 \tag{22}$$

$$\text{diag}(\mathbf{M}_{h_4}) = [1, 1, 1, (1-h_4), 1, 1, 1] \tag{23}$$

$$\mathbf{A}_1 = \mathbf{B}_4\mathbf{M}_{h_4}\mathbf{B}_3\mathbf{B}_2\mathbf{B}_1. \tag{24}$$

Biocontrol agents for garlic mustard include monophagous *Ceutorhynchus* weevils (Blossey et al. 2001, Davis et al. 2006, Gerber et al. 2009), most prominently *C. scrobicollis*. The effects of *C. scrobicollis* are modeled as a reduction in new seeds (by a proportion w_s) and second-year rosettes (by a proportion w_r) during season 4. We assume a linear relationship between these two effects with the ranges in Davis et al. (2006) (9–43% rosette mortality, 11–49% seed reduction; $w_r = 0.895w_s - 0.008$):

$$\text{diag}(\mathbf{M}_{w_4}) = [(1-w_s), 1, 1, (1-w_r), 1, 1, 1] \tag{25}$$

$$\mathbf{A}_1 = \mathbf{B}_4\mathbf{M}_{w_4}\mathbf{B}_3\mathbf{B}_2\mathbf{B}_1. \tag{26}$$

Bifurcation analysis

The effects of management were analyzed using bifurcation diagrams, which show the asymptotic population dynamics as a function of some parameter: in our case, as a harvest parameter is varied from 0 to 1 (0% to 100% mortality). Simulations at each value of the bifurcation parameter were run for 3000 seasons to achieve asymptotic dynamics. The densities (individuals per square meter) of rosettes plus adults, the stages with the most biomass and invasive impact, from an additional 300 seasons were plotted. Other parameters were maintained at the same values as in the unmanaged model.

Results: Dynamic responses to management

We present bifurcation diagrams (Fig. 3a) for the effects of each management strategy on season 2 (early summer) populations. This is the time of year when garlic mustard's invasive impacts are most significant, because season 2 has the highest densities of rosettes and adults (see Plate 1) and is the active growing season of many native species.

At low mortality for each strategy, managed populations exhibit the same interannual two-cycles as unmanaged populations. Increasing mortality results in a flip bifurcation (subcritical for fall herbicide, supercritical for all other strategies) that collapses each two-cycle into a single interannual equilibrium; this bifurcation point differs among strategies, occurring at the lowest level of management for spring herbicide (h_1). Very high levels of management mortality (>90% for h_1 and w_s, nearly 100% for the other strategies) are needed to reduce density to zero,

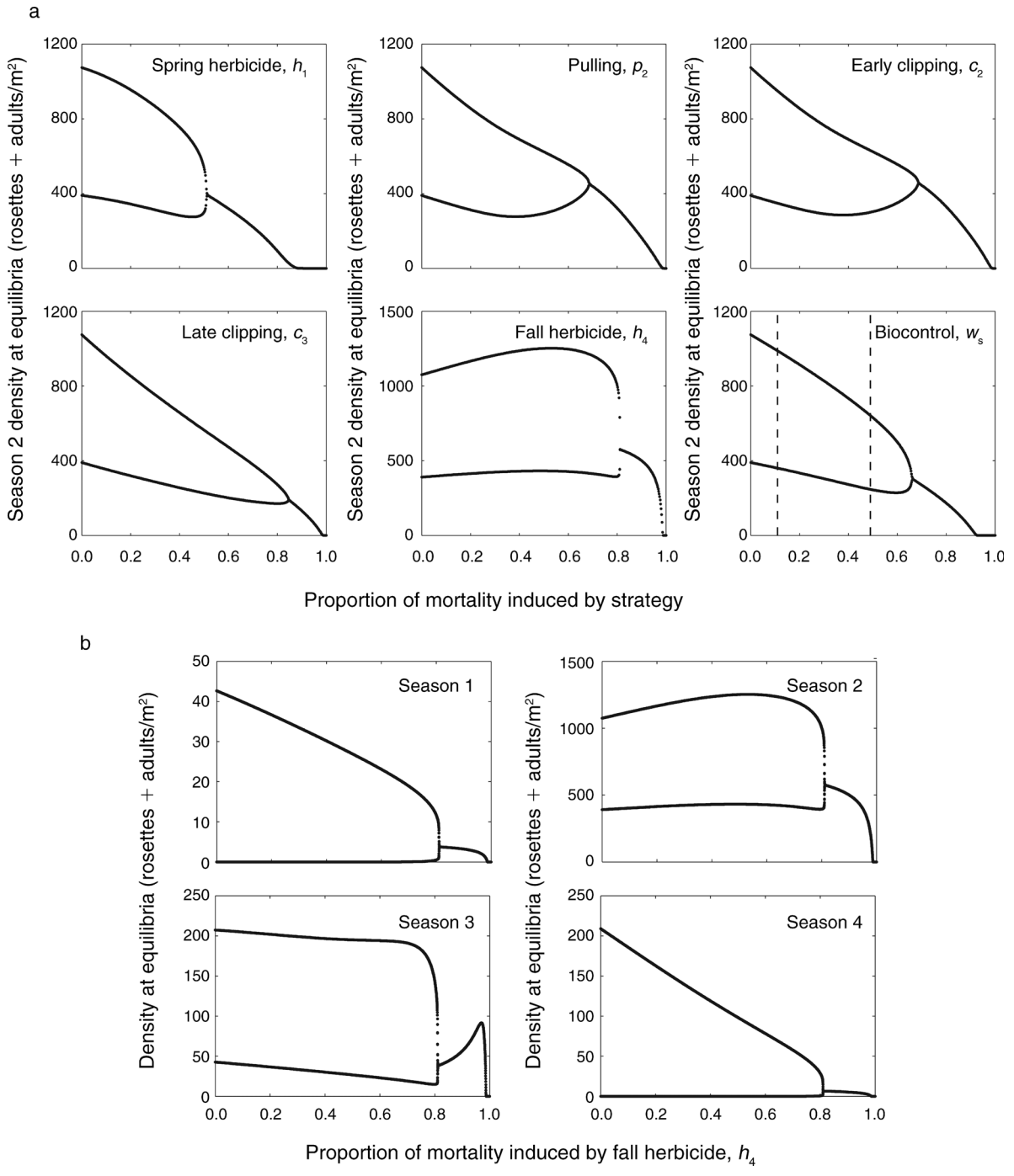

FIG. 3. (a) Bifurcation diagrams showing asymptotic garlic mustard densities under different management practices. The x-axis gives the proportion of mortality (0 to 1) induced by the given management strategy; the y-axis shows the corresponding population densities of rosettes plus adults pooled in season 2 (early summer). Dashed lines for the biocontrol parameter w_s indicate ranges for the weevil *Ceutorhynchus scrobicollis* (Davis et al. 2006). (b) Bifurcation diagrams for garlic mustard densities, in each season, under the fall herbicide treatment (h_4).

representing long-term eradication of the garlic mustard population.

Beyond these qualitative similarities, details of the response to increased management differ between strategies. Increasing fall herbicide mortality (h_4) from 0% to 70% actually increases densities in season 2, an example of overcompensation generated by density dependence (Fig. 3a). Conversely, increasing spring

herbicide mortality (h_1) consistently reduces density and eradicates the population at the lowest mortality of all the strategies. These results may explain why fall herbicide has been less effective than spring herbicide in reducing garlic mustard (Nuzzo 1991, Slaughter et al. 2007) and highlight the need to consider the seasonal timing of harvest.

Responses to harvest differ not only with the season of harvest, but also with the season of observation. While flip bifurcations and eradication occur at the same management levels regardless of season, other population dynamics can change significantly depending on the time of year. Increasing fall herbicide (h_4) from 80% to 95% mortality, for example, decreases densities in seasons 1, 2, and 4, but counteractively raises them in season 3 (Fig. 3b).

We note that management by pulling (p_2) or early clipping (c_2) of season 2 adults gives identical bifurcation diagrams (Fig. 3a), even though the latter strategy allows resprouts. This result may alleviate concerns about resprouts counteracting management (Pardini et al. 2008), potentially making early clipping favorable to more labor-intensive pulling.

Perturbation Analysis

Sensitivity of seasonal cycles

Fig. 3 uses bifurcation analysis to document qualitative changes in dynamics resulting from management mortality. However, the effects of changes in all of the demographic parameters may also be of interest. Perturbation analysis (sensitivity and elasticity) calculates the effects of such changes, which may be due to natural environmental change (including spatial differences between habitats or temporal change in environmental conditions), as well as management actions and other human impacts. The sensitivity of population density to mortalities, in particular, provides a way to measure compensatory effects. Whereas bifurcation analysis provides a qualitative picture of the global response to a single parameter, sensitivity analysis provides a quantitative measure of the local response to all parameters. Even though sensitivity and elasticity analyses are carried out using derivatives, it is well known that they provide useful information about the effects of even moderately large perturbations (Caswell 2001).

For a long time, perturbation analyses were available primarily for the growth rate of linear models (Caswell 1978, 2001). Because our model is nonlinear, the relevant index of population performance is the attractor to which population density asymptotically converges. This attractor may be either a fixed point or a cycle on the interannual time scale, both of which are cycles on the seasonal time scale. The necessary theory for the sensitivity of these attractors is developed in detail in Caswell (2008, 2009) and Caswell and Shyu (2012); for an introduction to matrix calculus methods and notation, see Appendix 1 of Caswell (2007).

To calculate the sensitivities of seasonal population densities, we must first determine the cycle of population vectors describing the asymptotic dynamics. A fixed point on the interannual time scale (as for a garlic mustard population under high management mortality) corresponds to a four-cycle on the seasonal time scale satisfying

$$\begin{aligned}
\hat{\mathbf{n}}_1 &= \mathbf{M}_1\mathbf{B}_4[\boldsymbol{\theta}_4,\ \hat{\mathbf{n}}_4]\ \hat{\mathbf{n}}_4 \\
\hat{\mathbf{n}}_2 &= \mathbf{M}_2\mathbf{B}_1[\boldsymbol{\theta}_1]\ \hat{\mathbf{n}}_1 \\
\hat{\mathbf{n}}_3 &= \mathbf{M}_3\mathbf{B}_2[\boldsymbol{\theta}_2,\ \hat{\mathbf{n}}_2]\ \hat{\mathbf{n}}_2 \\
\hat{\mathbf{n}}_4 &= \mathbf{M}_4\mathbf{B}_3[\boldsymbol{\theta}_3,\ \hat{\mathbf{n}}_1]\ \hat{\mathbf{n}}_3
\end{aligned} \tag{27}$$

where $\mathbf{M}_i$ refers to any management matrix with harvest occurring in season i.

If a population has more complex attracting dynamics, the set of seasonal population vectors must be expanded accordingly. A two-cycle on the interannual time scale (as for a garlic mustard population under low management mortality) corresponds to an eight-cycle on the seasonal time scale satisfying

$$\begin{aligned}
\hat{\mathbf{n}}_1 &= \mathbf{M}_1\mathbf{B}_4[\boldsymbol{\theta}_4, \hat{\mathbf{n}}_8]\hat{\mathbf{n}}_8 \quad & \hat{\mathbf{n}}_5 &= \mathbf{M}_1\mathbf{B}_4[\boldsymbol{\theta}_4, \hat{\mathbf{n}}_4]\hat{\mathbf{n}}_4 \\
\hat{\mathbf{n}}_2 &= \mathbf{M}_2\mathbf{B}_1[\boldsymbol{\theta}_1]\hat{\mathbf{n}}_1 & \hat{\mathbf{n}}_6 &= \mathbf{M}_2\mathbf{B}_1[\boldsymbol{\theta}_1]\hat{\mathbf{n}}_5 \\
\hat{\mathbf{n}}_3 &= \mathbf{M}_3\mathbf{B}_2[\boldsymbol{\theta}_2, \hat{\mathbf{n}}_2]\hat{\mathbf{n}}_2 & \hat{\mathbf{n}}_7 &= \mathbf{M}_3\mathbf{B}_2[\boldsymbol{\theta}_2, \hat{\mathbf{n}}_6]\hat{\mathbf{n}}_6 \\
\hat{\mathbf{n}}_4 &= \mathbf{M}_4\mathbf{B}_3[\boldsymbol{\theta}_3, \hat{\mathbf{n}}_1]\hat{\mathbf{n}}_3 & \hat{\mathbf{n}}_8 &= \mathbf{M}_4\mathbf{B}_3[\boldsymbol{\theta}_3, \hat{\mathbf{n}}_5]\hat{\mathbf{n}}_7.
\end{aligned} \tag{28}$$

For a system with k seasonal population vectors, each with s stages, define the product matrices $\mathbf{C}_1 \ldots \mathbf{C}_k$ so that

$$\hat{\mathbf{n}}_1 = \mathbf{M}_1\mathbf{B}_k\hat{\mathbf{n}}_k \tag{29}$$

$$= \mathbf{C}_k\hat{\mathbf{n}}_k \tag{30}$$

$$\hat{\mathbf{n}}_i = \mathbf{M}_i\mathbf{B}_{i-1}\hat{\mathbf{n}}_{i-1} \qquad i = 2, \ldots, k \tag{31}$$

$$= \mathbf{C}_{i-1}\hat{\mathbf{n}}_{i-1}. \tag{32}$$

To obtain the sensitivity of the $\hat{\mathbf{n}}_i$, differentiate Eqs. 30 and 32 with respect to $\boldsymbol{\theta}$ and apply the vec operator (which stacks the matrix columns into a column vector). For the four-cycle example in (27), the result is

$$\frac{d\hat{\mathbf{n}}_1}{d\boldsymbol{\theta}^\top} = (\hat{\mathbf{n}}_4^\top \otimes \mathbf{I}_s)\left(\frac{\partial \mathrm{vec}\mathbf{C}_4}{\partial \boldsymbol{\theta}^\top} + \sum_{j=1}^{4}\frac{\partial \mathrm{vec}\mathbf{C}_4}{\partial \hat{\mathbf{n}}_j^\top}\frac{d\hat{\mathbf{n}}_j}{d\boldsymbol{\theta}^\top}\right) + \mathbf{C}_4\left(\frac{d\hat{\mathbf{n}}_4}{d\boldsymbol{\theta}^\top}\right) \tag{33}$$

$$\frac{d\hat{\mathbf{n}}_i}{d\boldsymbol{\theta}^\top} = (\hat{\mathbf{n}}_{i-1}^\top \otimes \mathbf{I}_s)\left(\frac{\partial \mathrm{vec}\mathbf{C}_{i-1}}{\partial \boldsymbol{\theta}^\top} + \sum_{j=1}^{4}\frac{\partial \mathrm{vec}\mathbf{C}_{i-1}}{\partial \hat{\mathbf{n}}_j^\top}\frac{d\hat{\mathbf{n}}_j}{d\boldsymbol{\theta}^\top}\right) + \mathbf{C}_{i-1}\left(\frac{d\hat{\mathbf{n}}_{i-1}}{d\boldsymbol{\theta}^\top}\right) \qquad i = 2, \ldots, 4 \tag{34}$$

where $\otimes$ denotes the Kronecker product and $\mathbf{I}_s$ is a $s \times s$ identity matrix.

It is convenient to rewrite (34) using block matrices. We compile the seasonal population vectors in (27) into the vector

$$\mathbb{N} = \begin{pmatrix} \hat{\mathbf{n}}_1 \\ \hat{\mathbf{n}}_2 \\ \hat{\mathbf{n}}_3 \\ \hat{\mathbf{n}}_4 \end{pmatrix} \tag{35}$$

and define the matrices

$$\mathbf{H}_i = \hat{\mathbf{n}}_i^\top \otimes \mathbf{I}_s \qquad i = 1, \ldots, 4. \tag{36}$$

We write the block matrices

$$\mathbb{B} = \begin{pmatrix} 0 & 0 & 0 & \mathbf{C}_4 \\ \mathbf{C}_1 & 0 & 0 & 0 \\ 0 & \mathbf{C}_2 & 0 & 0 \\ 0 & 0 & \mathbf{C}_3 & 0 \end{pmatrix} \tag{37}$$

$$\mathbb{H} = \begin{pmatrix} 0 & 0 & 0 & \mathbf{H}_4 \\ \mathbf{H}_1 & 0 & 0 & 0 \\ 0 & \mathbf{H}_2 & 0 & 0 \\ 0 & 0 & \mathbf{H}_3 & 0 \end{pmatrix} \tag{38}$$

$$\mathbb{C} = \begin{pmatrix} \dfrac{\partial \mathrm{vec}\mathbf{C}_1}{\partial \mathbf{n}_1^\top} & \cdots & \dfrac{\partial \mathrm{vec}\mathbf{C}_1}{\partial \mathbf{n}_4^\top} \\ \vdots & \ddots & \vdots \\ \dfrac{\partial \mathrm{vec}\mathbf{C}_4}{\partial \mathbf{n}_1^\top} & \cdots & \dfrac{\partial \mathrm{vec}\mathbf{C}_4}{\partial \mathbf{n}_4^\top} \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & \dfrac{\partial \mathrm{vec}\mathbf{C}_2}{\partial \mathbf{n}_2^\top} & 0 & 0 \\ \dfrac{\partial \mathrm{vec}\mathbf{C}_3}{\partial \mathbf{n}_1^\top} & 0 & 0 & 0 \\ 0 & 0 & 0 & \dfrac{\partial \mathrm{vec}\mathbf{C}_4}{\partial \mathbf{n}_4^\top} \end{pmatrix} \tag{39}$$

$$\mathbb{D} = \begin{pmatrix} \dfrac{\partial \mathrm{vec}\mathbf{C}_1}{\partial \boldsymbol{\theta}^\top} \\ \dfrac{\partial \mathrm{vec}\mathbf{C}_2}{\partial \boldsymbol{\theta}^\top} \\ \dfrac{\partial \mathrm{vec}\mathbf{C}_3}{\partial \boldsymbol{\theta}^\top} \\ \dfrac{\partial \mathrm{vec}\mathbf{C}_4}{\partial \boldsymbol{\theta}^\top} \end{pmatrix}. \tag{40}$$

The structures of $\mathbb{B}$, $\mathbb{H}$, and $\mathbb{D}$ depend only on the period of the seasonal cycle. However, the matrix $\mathbb{C}$ in (39) is determined by the density dependencies in each of the $\mathbf{C}_i$. In the case of garlic mustard, $\mathbf{C}_2$, $\mathbf{C}_3$, and $\mathbf{C}_4$ depend only on $\mathbf{n}_2$, $\mathbf{n}_1$, and $\mathbf{n}_4$, respectively, making the corresponding derivatives the only nonzero entries in $\mathbb{C}$.

The matrix $d\mathbb{N}/d\boldsymbol{\theta}^\top$ contains the sensitivity of every stage in each season (all the entries of $\mathbb{N}$) to every parameter in $\boldsymbol{\theta}$, and is given by

$$\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\top} = \left(\frac{dn_i}{d\theta_j}\right) \tag{41}$$

$$= [\mathbf{I}_{ks} - \mathbb{B} - \mathbb{H}\mathbb{C}]^{-1}\mathbb{H}\mathbb{D} \tag{42}$$

where $\mathbf{I}_{ks}$ is a $ks \times ks$ identity matrix (see Caswell 2008, Caswell and Shyu 2012).

The corresponding matrix of elasticities is

$$\frac{\varepsilon\mathbb{N}}{\varepsilon\boldsymbol{\theta}^\top} = \left(\frac{\theta_j}{n_i}\frac{dn_i}{d\theta_j}\right) \tag{43}$$

$$= \mathrm{diag}(\mathbb{N})^{-1}\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\top}\mathrm{diag}(\boldsymbol{\theta}). \tag{44}$$

Depending on the management criteria, it may be convenient to obtain the sensitivities of the average densities taken over multiple stages or seasons. To calculate sensitivities of weighted average stage densities, define $\mathbf{c}$ as a vector of weights for each stage (as based on stage biomass, harvest value, etc.) and $\hat{N}_i = \mathbf{c}^\top\hat{\mathbf{n}}_i$ as the weighted average stage density (scalar) for phase i of the population vector cycle. Then,

$$\frac{d\hat{\mathbf{N}}}{d\boldsymbol{\theta}^\top} = (\mathbf{I}_s \otimes \mathbf{c}^\top)\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\top}. \tag{45}$$

To calculate sensitivities of weighted-average seasonal densities (e.g., annually averaged densities), define $\mathbf{b}$ as a vector of weights for each season (e.g., their relative lengths) and $\bar{\mathbf{n}} = \sum_{i=1}^{k} b_i\hat{\mathbf{n}}_i$ as the seasonally averaged population vector. Then

$$\frac{d\bar{\mathbf{n}}}{d\boldsymbol{\theta}^\top} = (\mathbf{b}^\top \otimes \mathbf{I}_k)\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\top}. \tag{46}$$

To calculate both stage- and seasonally averaged sensitivities, take the seasonal averages of the weighted average stage values to obtain $\bar{N} = \sum_{i=1}^{k} b_i\mathbf{c}^\top\hat{\mathbf{n}}_i$. Then

$$\frac{d\bar{N}}{d\boldsymbol{\theta}^\top} = (\mathbf{b}^\top \otimes \mathbf{c}^\top)\frac{d\mathbb{N}}{d\boldsymbol{\theta}^\top}. \tag{47}$$

For the garlic mustard model, we consider the sensitivities and elasticities of stage-averaged population densities (number of rosettes plus adults, equally weighted, per square meter) to demographic and management parameters. These sensitivities and elasticities are found for the seasonal and annually averaged densities of an initially unmanaged population.

Results: Effects of management and demographic perturbations

Perturbation analyses can reveal when management in one season has different effects in other seasons. As shown in Fig. 4a, unmanaged populations experience one series of seasonal densities in the first year of each

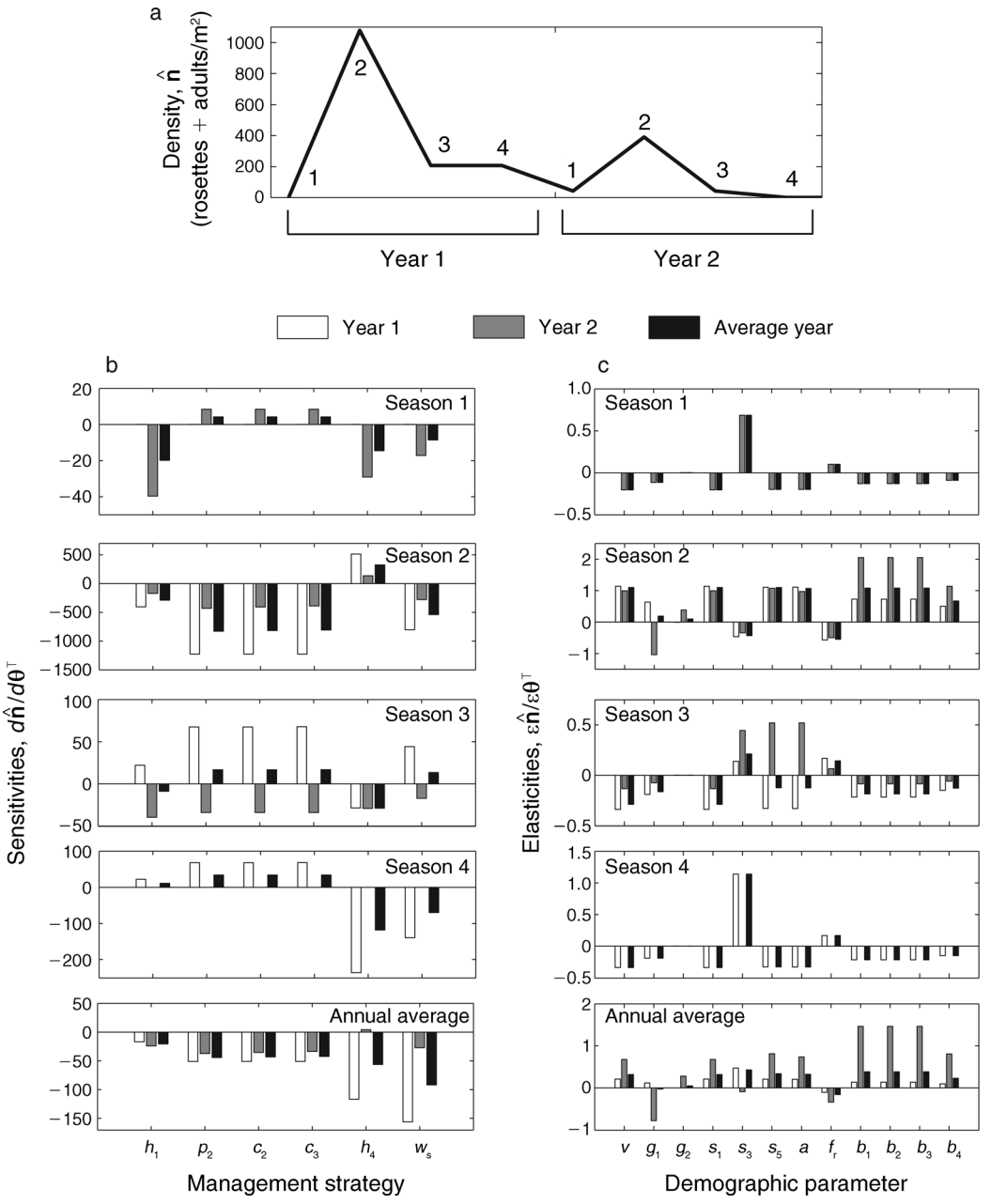

FIG. 4. (a) Densities (number of rosettes plus adults per square meter) in an unmanaged population over the interannual two-cycle (seasonal eight-cycle). Seasons 1–4 along the line correspond to spring, early summer, late summer, and fall/winter as in Fig. 1. (b) Sensitivities of the eight seasonal densities in panel (a), and of the average annual density, to management parameters shown in Fig. 3. (c) Elasticities of these densities to demographic parameters listed in Table 1; for these analyses, populations are initially unmanaged (all management parameters at 0).

interannual two-cycle (year 1) and a different series of densities in the second year (year 2). These densities (in terms of rosettes plus adults) reach their maximum in season 2 (early summer) of year 1 and then fall to zero in season 4 of year 2 and season 1 of year 1 (fall to spring).

The sensitivities of these densities to management perturbations, and their elasticities to demographic perturbations, are shown in Fig. 4b, c. These results indicate that perturbations that decrease densities in one season may not affect, or will even increase, densities at other times of year. As a result, optimal management strategies may shift depending on the season(s) of interest. For example, the maximum garlic mustard population (year 1, season 2 in Fig. 4a) has large positive elasticities to seed viability (v), seedling survival (s_1), second-year rosette spring survival (s_5), and the flowering-to-fruiting adult transition (a) (Fig. 4c). These transitions may accordingly be effective targets for

mitigating the maximum density, although some may be easier to perturb than others (changing seed viability, for instance, is probably unfeasible). Most of the perturbations that reduce the maximum density also reduce the average annual density. However, although the average density has its largest positive elasticity to the survival of first-year rosettes in late summer (s_3), the maximum density has a negative elasticity to s_3. Thus, while killing summertime rosettes may be the most effective way to reduce the average annual density, it would do so at the cost of raising the maximum seasonal density.

Positive sensitivities of density to management perturbations reveal overcompensatory effects of the management harvest (i.e., increasing the mortality increases, rather than decreases, population density). Our sensitivity results show that increasing fall herbicide (h_4) would increase season 2 densities in both year 1 and 2 (as previously noted from the bifurcation results). Similarly, spring herbicide (h_1) would increase seasons 3 and 4 densities in year 1, while pulling (p_2) and clipping (c_2, c_3) would increase densities in season 1 of both years and in seasons 3 and 4 of year 1.

Discussion

Many species are affected by seasonal density-dependent processes. These processes may interact with management to produce complex, potentially counter-intuitive dynamics. The model that we present here accommodates seasonal and interannual variability, density dependence, arbitrary stages, and harvest, as well as delayed density effects (Ratikainen et al. 2008). This approach also provides substantial detail about how population structure in each season will respond to perturbations. In particular, Eqs. 42 and 44 give the sensitivities and elasticities, respectively, of every stage in every season to every parameter in the model (whether demographic or management-based). Using Eqs. 45, 46, and 47, one can also calculate the sensitivity of population densities averaged over stages, seasons, or both.

When applied to garlic mustard, our model produces biennial oscillations similar to those observed in unmanaged populations. Bifurcation and perturbation analyses demonstrate that the seasonal timing of harvest affects long-term densities, and that some strategies drive compensation or overcompensation in certain seasons. Previous nonlinear models for garlic mustard (Pardini et al. 2009, 2011) have also suggested potential overcompensatory responses to management. Our periodic model elucidates the seasonal harvest strategies under which overcompensation occurs and quantifies seasonal population increases using sensitivity analysis. Because management effects in one season can produce different, and even opposing, effects at other times of year, control programs should consider season specificity in both management objectives and actions. An optimal harvest strategy may depend on whether managers prioritize season-specific goals (e.g., reduced densities in season 2) or more evenly distributed density reductions throughout the year. The concept of "density" here deserves some additional discussion. It is often interpreted as total numbers, but in a structured population, total numbers may be irrelevant if different stages produce very different impacts because of differences in size, behavior, energetics, or other factors (Caswell 2008). These impacts can be incorporated into sensitivity calculations through the weighting vectors in Eqs. 45–47. Our definition of density in terms of rosettes and adults uses a particular case of such a weighting vector.

Even more interesting is the potential ability to incorporate nonlinear measures of impact (e.g., Yokomizo et al. 2009). Suppose that the impact of an invasive species is given by a function $u = f(\mathbb{N})$ of the population vector $\mathbb{N}$. The function $f(\cdot)$ might reflect an accelerating response, in which the invasive species has little effect until it reaches some threshold density, or a decelerating response, in which there is a rapidly increasing effect at low densities, but no further increase at higher densities. The sensitivity of the impact u to model parameters can be written directly as

$$\frac{du}{d\boldsymbol{\theta}^{\top}} = \frac{d\mathbb{N}}{d\boldsymbol{\theta}^{\top}} \frac{du}{d\mathbb{N}} \tag{48}$$

where $d\mathbb{N}/d\boldsymbol{\theta}^{\top}$ is given by (42). This calculation invites the explicit quantification of the impacts of invasive species, which will certainly involve not only purely biological effects, but also social and bioeconomic concerns.

Indeed, while population models can identify potentially promising strategies, managers must also consider factors such as cost and feasibility. Given a goal of reducing season 2 densities, one might reason from Fig. 3a that all strategies, except for fall herbicide (h_4), give qualitatively similar results and should have equal priority for implementation. In practice, however, pulling (p_2) and late clipping (c_3) are labor intensive compared to the other treatments, whereas biocontrol (w_s) is limited by its agents. We find that *C. scrobicollis*, for instance, would not even push populations past the flip bifurcation, even though our assumption of fixed biocontrol mortality probably overestimates biocontrol's long-term efficacy. When all of these factors are taken into account, spring herbicide (h_1) and early clipping (c_2) might emerge as the most practical options. Results from models like ours can be used to inform related cost considerations (for examples of sensitivity analyses that incorporate economic costs, see Baxter et al. 2006).

Although our results focus on asymptotic dynamics, a population may need a significant amount of time to converge to its long-term behavior. Our model simulations suggest that an initially unmanaged population will take 5–10 years to reach its new attractor under management (results not shown). As a result, evaluating the management effects that we have

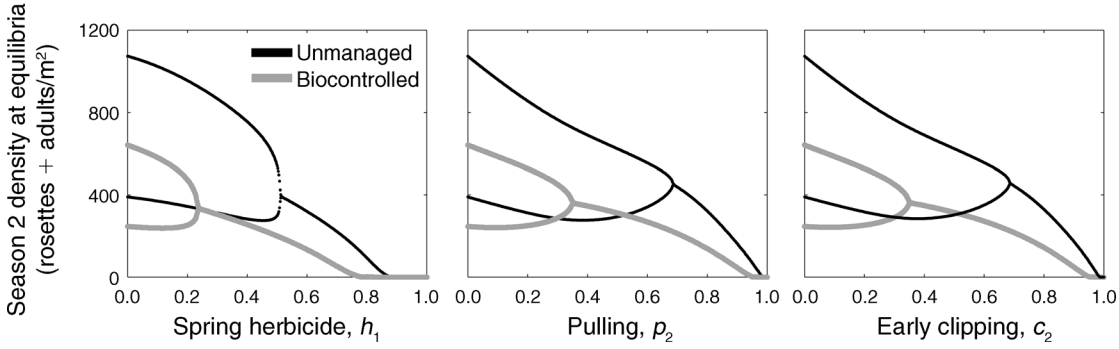

FIG. 5. Bifurcation diagrams showing the effects of spring herbicide, pulling, and early clipping when paired with highly effective biocontrol (proportional reduction in new seeds, $w_s = 0.43$; proportional reduction in rosettes, $w_r = 0.49$). Initially unmanaged populations are in black. Populations initially at the new attractor under biocontrol are in gray.

projected may require population monitoring over time scales at least this long. It may accordingly be useful to simulate transient dynamics, especially in an adaptive management context. Although all treatments can be stopped if populations are eradicated, only spring herbicide (h_1) and biocontrol (w_s) achieve eradication at less than near 100% annual mortality (Fig. 3a), and even these strategies require at least 90% annual mortality, over a period of decades, to reduce the long-lived seed bank to negligible levels. It may thus be more feasible to retain densities at manageable levels through annual harvest, rather than to attempt eradication.

As with many pest control models, we describe management tactics as factors that influence mortality, but have no individual dynamics. Biocontrol agents, however, are populations in their own right, and their effects may depend on feedback from the target species. The effectiveness of *C. scrobicollis*, for example, might decrease with the density of garlic mustard, and seasons with low aboveground biomass (e.g., season 4 of year 2 and season 1 of year 1 in Fig. 4a) might lead to local extinctions of the biocontrol agent. Accounting for these interactions would require a fully coupled two-species model for the biocontrol agent and target species (e.g., Buckley et al. 2005).

Several additional management options deserve further consideration. One option is to simultaneously implement multiple strategies. In the presence of highly effective constant biocontrol ($w_s = 0.43$, $w_r = 0.49$), we find that all five other strategies reach the flip bifurcation (and, in some cases, population eradication) at lower management levels (Fig. 5), suggesting that combining management efforts may help to achieve difficult control goals. Another possibility is to alternate strategies between years. As sensitivities and elasticities vary for year 1 and year 2 populations (Fig. 4b and c), differential treatments every other year may more effectively reduce target populations. Based on the number and placement of management matrices in the annual matrix product, our modeling framework can be used to analyze these more complex harvest programs.

Because conclusions from any analyses of population management strategies are projections conditional upon model structure and parameter values (Caswell 2001:626), their generality depends on how widely applicable their model structure and parameters are. The structure of our model (Fig. 1) applies generally to garlic mustard in North American temperate forests. Parameter values in other habitats, however, will differ from those measured in our Missouri field population (Table 1). Our modeling framework could be reapplied to other garlic mustard populations with sufficient demographic data. Even in the absence of such data for other populations, our results still provide qualitative insights about responses to management (e.g., seasonal differences, compensatory effects) that can inform control efforts. Many of our qualitative findings (bifurcations of interannual two-cycles into single equilibria with increasing harvest, compensatory behavior for h_4 in season 2, and so forth) are robust to a range of North American parameter values (e.g., those from Evans and Davis 2011).

Our approach is also applicable to other harvest scenarios. In addition to controlling invasive pests, harvest events affect the sustainability of resource populations and can be important even when unintentional, as in the case of incidental bycatch or ship strikes. Forecasting population responses in these situations is crucial for developing effective management policies. Compensatory responses have been documented for many resource species, including waterfowl and game animals (e.g., Burnham and Anderson 1984, Nichols et al. 1984). In such cases, compensation allows "surplus" individuals to be harvested without changing the remaining population size, whereas overcompensation leads to maximum population densities at intermediate harvest levels. By explicitly including seasonality and density dependence, models like ours can provide insight

PLATE 1. *Alliaria petiolata* can reach high densities when it invades forests, the effects of which are especially dramatic in season 2 (early summer). The photo shows adult plants in May at Howell Island Conservation Area, St. Louis County, Missouri, USA. Photo credit: E. A. Pardini.

into the management of resource, pest, and conserved populations alike.

ACKNOWLEDGMENTS

This work was supported by the National Science Foundation (grant DEB-0816514), the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service (grant 05-2290), the Alexander von Humboldt Foundation, and the Academic Programs Office at WHOI. H. Caswell is grateful to the Max Planck Institute for Demographic Research for its hospitality and extends thanks to the staff at Samtrot. We also thank John Drake, Jon Chase, and Britta Teller for their contributions to the development of the garlic mustard model and data collection.

LITERATURE CITED

Anderson, R. C., S. S. Dhillion, and T. M. Kelley. 1996. Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*) in central Illinois. Restoration Ecology 4:181–191.

Åström, M., P. Lundberg, and S. Lundberg. 1996. Population dynamics with sequential density-dependencies. Oikos 75:174–181.

Baxter, P. W. J., M. A. McCarthy, H. P. Possingham, P. W. Menkhorst, and N. McLean. 2006. Accounting for management costs in sensitivity analyses of matrix population models. Conservation Biology 20:893–905.

Blossey, B., V. Nuzzo, H. Hinz, and E. Gerber. 2001. Developing biological control of *Alliaria petiolata* (M.Bieb.) Cavara and Grande (garlic mustard). Natural Areas Journal 21:357–367.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–426.

Buckley, Y. M., H. L. Hinz, D. Matthies, and M. Rees. 2001. Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). Ecology Letters 4:551–558.

Buckley, Y. M., M. Rees, A. W. Sheppard, and M. J. Smyth. 2005. Stable coexistence of an invasive plant and biocontrol agent: a parameterized coupled plant–herbivore model. Journal of Applied Ecology 42:70–79.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology 65:105–112.

Cameron, T. C., and T. G. Benton. 2004. Stage-structured harvesting and its effects: an empirical investigation using soil mites. Journal of Animal Ecology 73:996–1006.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology 14:215–230.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.
Caswell, H. 2007. Sensitivity analysis of transient population dynamics. Ecology Letters 10:1–15.
Caswell, H. 2008. Perturbation analysis of nonlinear matrix population models. Demographic Research 18:59–116.
Caswell, H., and E. Shyu. 2012. Sensitivity analysis of periodic matrix models. Theoretical Population Biology 82:329–339.
Cavers, P. B., M. I. Heagy, and R. F. Kokron. 1979. The biology of Canadian weeds. 35. *Alliaria petiolata* (M. Bieb.) Cavara and Grande. Canadian Journal of Plant Science 59:217–229.
Davis, A. S., D. A. Landis, V. Nuzzo, B. Blossey, E. Gerber, and H. L. Hinz. 2006. Demographic models inform selection of biocontrol agents for garlic mustard (*Alliaria petiolata*). Ecological Applications 16:2399–2410.
Evans, J. A., and A. S. Davis. 2011. Consequences of parameterization and structure of applied demographic models: a comment on Pardini et al. (2009). Ecological Applications 21:608–613.
Gerber, E., G. Cortat, H. L. Hinz, B. Blossey, E. Katovich, and L. Skinner. 2009. Biology and host specificity of *Ceutorhynchus scrobicollis* (Curculionidae; Coleoptera), a root-crown mining weevil proposed as a biological control agent against *Alliaria petiolata* in North America. Biocontrol Science and Technology 19:117–138.
Hinz, H. L., and E. Gerber. 1998. Investigations on potential biological control agents of garlic mustard *Alliaria petiolata* (Bieb.) Cavara and Grande. Annual Report for 1998. CABI Bioscience, Delemont, Switzerland.
Jonzén, N., and P. Lundberg. 1999. Temporally structured density-dependence and population management. Annales Zoologici Fennici 36:39–44.
Jonzén, N., B. A. Nolet, L. Santamara, and M. G. E. Svensson. 2002. Seasonal herbivory and mortality compensation in a swan–pondweed system. Ecological Modeling 147:209–219.
Kokko, H., and J. Lindström. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. Ecological Modelling 110:293–304.
Kot, M., and W. M. Schaeffer. 1984. The effects of seasonality on discrete models of population growth. Theoretical Population Biology 26:340–360.
Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. North American Wildlife and Natural Resources Conference 49:535–554.
Nicholson, A. J. 1957. The self-adjustment of populations to change. Cold Spring Harbor Symposia on Quantitative Biology 22:153–173.
Nuzzo, V. A. 1991. Experimental control of garlic mustard [*Alliaria petiolata* (Bieb.) Cavara and Grande] in northern Illinois using fire, herbicide, and cutting. Natural Areas Journal 11:158–167.
Nuzzo, V. A. 2000. Elemental stewardship abstract for *Alliaria petiolata* (*Alliaria officinalis*) garlic mustard. Prepared for The Nature Conservancy, Arlington, Virginia, USA. http://www.invasive.org/weedcd/pdfs/tncweeds/allipet.pdf
Pardini, E. A., J. M. Drake, J. Chase, and T. M. Knight. 2009. Complex population dynamics and control of the invasive biennial *Alliaria petiolata* (garlic mustard). Ecological Applications 19:387–397.
Pardini, E. A., J. M. Drake, and T. M. Knight. 2011. On the utility of population models for invasive plant management: response to Evans and Davis. Ecological Applications 21:614–618.
Pardini, E. A., B. J. Teller, and T. M. Knight. 2008. Consequences of density dependence for management of stage-structured invasive plant (*Alliaria petiolata*). American Midland Naturalist 160:310–322.
Ratikainen, I. I., J. A. Gill, T. G. Gunnarsson, W. J. Sutherland, H. Kokko. 2008. Why density-dependence is not instantaneous: theoretical developments and management implications. Ecology Letters 11:184–198.
Roberts, H. A., and J. E. Boddrell. 1983. Seed survival and periodicity of seedling emergence in eight species of Cruciferae. Annals of Applied Biology 103:301–304.
Sinclair, A. R. E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75:164–173.
Slaughter, B. S., W. W. Hochstedler, D. L. Gorchov, and A. M. Carlson. 2007. Response of *Alliaria petiolata* (garlic mustard) to five years of fall herbicide application in a southern Ohio deciduous forest. Journal of the Torrey Botanical Society 134:18–26.
Smith, M., H. Caswell, and P. Mettler-Cherry. 2005. Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. Ecological Applications 15:1036–1052.
Solis, K. 1998. Update: new results indicate flowering garlic mustard should be bagged and destroyed (Wisconsin). Restoration and Management Notes 16:223–224.
Tang, S., and L. Chen. 2004. The effect of seasonal harvesting on stage-structured population models. Journal of Mathematical Biology 48:357–374.
Winterer, J., M. C. Walsh, M. Poddar, J. W. Brennan, and S. M. Primak. 2005. Spatial and temporal segregation of juvenile and mature garlic mustard plants (*Alliaria petiolata*) in a central Pennsylvania woodland. American Midland Naturalist 153:209–216.
Yokomizo, H., H. P. Possingham, M. B. Thomas, and Y. M. Buckley. 2009. Managing the impact of invasive species: the value of knowing the density–impact curve. Ecological Applications 19:376–386.
Zipkin, E. F., C. E. Kraft, E. G. Cooch, and P. J. Sullivan. 2009. When can efforts to control nuisance and invasive species backfire? Ecological Applications 19:1585–1595.
Zipkin, E. F., P. J. Sullivan, E. G. Cooch, C. E. Kraft, B. J. Shuter, and B. C. Weidel. 2008. Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition? Canadian Journal of Fisheries and Aquatic Sciences 65:2279–2292.

Supplemental Material

Supplement

Annotated MATLAB code for the garlic mustard time series simulations (Fig. 2), bifurcation diagrams (Figs. 3 and 5), and sensitivity analysis (Fig. 4) (*Ecological Archives* A023-091-A1).